NEOTROPICAL BIOLOGY AND CONSERVATION

Neotropical Biology and Conservation 21(1): 49–66 (2026)
DOI: 10.3897/neotropical.21.e183324

Research Article

Unveiling the ghost: short-eared dog (*Atelocynus microtis*) distribution, activity patterns, habitat use, relative abundance, and occupancy in Bolivia

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Abstract

The short-eared dog (*Atelocynus microtis*) is one of the world's least-known canids and one of Latin America's least-known carnivores. We performed a systematic summary of published and unpublished distributional records for the species across Bolivia (*n* = 500), and between 2001 and 2024, we ran 34 intensive camera-trap surveys across the lowland portions of the Greater Madidi-Tambopata Landscape (northwestern Bolivia and southeastern Peru) and the Llanos de Moxos Biocultural Landscape (northern Bolivia), which resulted in 594 independent events for the short-eared dog. Short-eared dogs were primarily diurnal, with camera-trap capture frequencies of 0.18–2.4 independent events per 100 camera-trap nights across 21 (61.8%) of the 34 surveys. A comparison with camera-trap data from ocelots (*Leopardus pardalis*) extrapolated an average density of 15 individuals/100 km^2, suggesting that short-eared dogs are less abundant than other medium-sized carnivores but more abundant than larger-bodied carnivores (e.g., jaguar). Our results reveal variation in short-eared dog relative abundance and occupancy between survey sites and over time. Occupancy analyses emphasized a strong preference for intact forest, underscoring the importance of protected areas and other management units that preserve forest cover in the Amazon.

Key words: Activity patterns, Bolivia, camera trapping, capture frequencies, distribution, Peru

OPEN ACCESS

Academic editor: Piter Boll
Received: 23 December 2025
Accepted: 4 March 2026
Published: 27 March 2026

ZooBank: https://zoobank.org/D912088C-3572-4FEB-BDC7-91D83AC7518F

Citation: Wallace RB, Ayala G, Viscarra M, Porcel Z (2026) Unveiling the ghost: short-eared dog (*Atelocynus microtis*) distribution, activity patterns, habitat use, relative abundance, and occupancy in Bolivia. Neotropical Biology and Conservation 21(1): 49–66. https://doi.org/10.3897/neotropical.21.e183324

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Introduction

The short-eared dog (*Atelocynus microtis*), or ghost dog, is perhaps the least known medium- to large-sized Neotropical mammal (Berta 1986; Eisenberg 1989; Peres 1991; Emmons and Feer 1990) and potentially one of the scarcest canids (Ginsberg and Macdonald 1990; Leite and Williams 2004; Leite Pitman and Williams 2011). Even the geographical and habitat distribution of this species is unclear (Leite Pitman and Williams 2011; Rocha et al. 2020), with its ecology virtually unknown (Peres 1991; Leite and Williams 2004; Michalski 2010; Wallace et al. 2010a; Leite Pitman and Williams 2011; Rocha et al. 2020). After decades of speculation, more recent continental-scale habitat analyses suggest that short-eared dogs are forest specialists (Rocha et al. 2020), with

occupancy studies in southern Peru suggesting a strong preference for *terra firme*, or upland forests away from rivers (Leite Pitman et al. 2026; Zwicker, unpublished data). Until recently, there were only six reported localities in Bolivia, four museum specimens (Anderson 1997), and two direct observations by experienced field biologists (Parker and Bailey 1991; Emmons 1998). However, subsequent efforts to systematize national information on mammals (Wallace et al. 2010a, 2010b, 2013a) and carnivores (Wallace et al. 2013b) revealed substantially more confirmed localities for the species (n = 64).

Given the paucity of information regarding this elusive canid, we provide an updated summary regarding its known distribution across Bolivia, as well as its activity patterns, relative abundance, and occupancy gathered during 25 years of fieldwork in northern and central Bolivia, including 34 camera-trapping surveys primarily designed to assess jaguar (*Panthera onca*) densities (Wallace et al. 2003; Silver et al. 2004; Ayala et al. 2022).

Methods

Distribution

Data from multiple sources were used in our efforts to describe the distribution of short-eared dogs in Bolivia within the framework of a national-scale effort on medium- to large-sized mammals (Wallace et al. 2010b, 2013a). First, we systematized historical records for the species, including published literature and gray, unpublished documents on mammals from seven Bolivian libraries. Second, we summarized observations of short-eared dogs, camera-trap photographs, and other signs (e.g., tracks) recorded over 25 years of field research in the Greater Madidi-Tambopata Landscape and the Llanos de Moxos Biocultural Landscape. To ensure the independence of camera-trap data, these records of species presence were filtered, and a single presence record per sampling unit (camera-trap station) per sampling year was selected. Third, between 2001 and 2010, we conducted interviews with park guards across the five national protected areas of the Greater Madidi-Tambopata Landscape about target wildlife presence, including short-eared dogs, using enlarged satellite images (1 km^2 grid) of the region. Fourth, during the same years, we conducted wildlife presence interviews using the same maps across 16 communities in the two Tacana Indigenous Territories of northern La Paz. All distribution points were georeferenced to generate a GIS (Geographic Information System) database of wildlife records, including short-eared dogs. For records lacking altitude data, altitude was extrapolated from a digital elevation model (Jarvis et al. 2008).

Camera trapping study sites

Thirty-four camera-trap surveys were conducted at 23 study sites across two conservation regions: the Greater Madidi-Tambopata Landscape, an approximately 111,000 km^2 binational area in northwestern Bolivia and southeastern Peru, and the Llanos de Moxos Biocultural Landscape, a 120,000–130,000 km^2 area in northern Bolivia (Table 1). The Bolivian study sites (n = 20) are in the Iturralde Province of the La Paz Department, as well as the José Ballivián, Yacuma, and Marbán provinces of the Beni Department. The Peruvian study sites (n = 3) are

Table 1. Habitat and ecoregion for 23 camera-trap survey areas in Bolivia and Peru sampled between 2001 and 2024.

Conservation landscape	Country	General survey area	Habitat	Ecoregion
Greater Madidi-Tambopata	Bolivia	Tuichi River	Amazonian Forest	Sub-Andean / Pre-Andean Amazonian Forests
		Hondo River	Amazonian Forest	Sub-Andean / Pre-Andean Amazonian Forests
		Quendeque River	Amazonian Forest	Sub-Andean / Pre-Andean Amazonian Forests
		Madidi River	Amazonian Forest	Amazonian Forest & Inundated Moxos Savanna
		Heath River	Amazonian Forest	Pando Amazonian Forest & Inundated Moxos Savanna
		Undumo River	Amazonian Forest	Amazonian Forest & Inundated Moxos Savanna
		Tequeje River	Amazonian Forest	Amazonian Forest & Inundated Moxos Savanna
		Quiquibey River	Amazonian Forest	Sub-Andean / Pre-Andean Amazonian Forests
		Pampas de Apolo	Lower-Mid Montane Forest	Yungas & Sub-Andean / Pre-Andean Amazonian Forests
		Sipia	Lower-Mid Montane Forest	Yungas & Sub-Andean / Pre-Andean Amazonian Forests
		Mamacona	Lower-Mid Montane Forest	Yungas & Sub-Andean / Pre-Andean Amazonian Forests
		Sarayoj	Lower-Mid Montane Forest	Yungas & Sub-Andean / Pre-Andean Amazonian Forests
		Death Road	Lower-Mid Montane Forest	Yungas & Sub-Andean / Pre-Andean Amazonian Forests
	Peru	Chuncho River	Amazonian Forest	Sub-Andean / Pre-Andean Amazonian Forests
		Tambopata River	Amazonian Forest	Sub-Andean / Pre-Andean Amazonian Forests
		Malinowski River	Amazonian Forest	Sub-Andean / Pre-Andean Amazonian Forests
Llanos de Moxos Biocultural	Bolivia	Mojon-Santiago	Amazonian Forest & Natural Savanna	Inundated Moxos Savanna, Cerrado, & Inundated Amazonian Forest
		Grandes Lagos Tectónicos de Exaltación	Amazonian Forest & Natural Savanna	Inundated Moxos Savanna, Cerrado, & Inundated Amazonian Forest
		Reyes – Santa Rosa del Yacuma	Amazonian Forest & Natural Savanna	Inundated Moxos Savanna, Cerrado, & Inundated Amazonian Forest
		Biata – Yata – Benicito	Amazonian Forest & Natural Savanna	Inundated Moxos Savanna, Cerrado, & Inundated Amazonian Forest
		Isiboro – Pojige – Anteojos	Amazonian Forest & Natural Savanna	Inundated Moxos Savanna, Cerrado, & Inundated Amazonian Forest

found in the Madre de Dios Region. Four of the 23 survey sites were sampled multiple times: Tuichi-Hondo (n = 7; 2001, 2002, 2008, 2012, 2014, 2019, and 2023), the Upper Madidi (n = 4; 2004, 2011, 2015, and 2022), the Lower Heath (n = 2; 2005 and 2017), and the Quiquibey (n = 2; 2008 and 2019).

The region's annual mean precipitation is 2,000–3,000 mm, and the annual mean temperature is 26 °C, with significant climatic variability and a marked dry season between May and October (Fuentes 2005). While all survey sites were in the Amazonian region, with the majority in the Sub-Andean/Pre-Andean Amazonian Forest ecoregion, exceptions included Inundated Moxos Savanna, Yungas, Inundated Amazonian Forest, and Cerrado (Ibisch et al. 2003; Table 1). Tropical forests were riverine and adjacent *terra firme* forests, characterized by relatively high diversity, high canopy heights (30–40 m), and high densities of diverse palm species.

Camera-trapping methods

Jaguar surveys

Most camera-trapping efforts were initially established as surveys to estimate and monitor jaguar (*Panthera onca*) population density (Wallace et al. 2003; Ayala et al. 2020, 2022; Table 2). During initial visits to each study area, we identified potential sites for camera-trap placement using the presence of jaguar signs (e.g., recent tracks), which were then mapped in GIS, with final sites selected using a 1.6–2 km minimum distance between points (Wallace et al. 2003; Silver et al. 2004; Wallace et al. 2012; Ayala et al. 2020, 2022). We classified each camera-trap station into one of three habitat types: a) **Beach**, open areas along primary and secondary rivers with associated lagoons and oxbow lakes; b) **Forest**, stations positioned within the forest, often on recently built trails, identified animal trails, and/or small streams (< 3 m wide) within the forest; and c) **Pampas**, open lowland tropical grasslands.

Each year, camera trapping was conducted during the dry season, except at Hondo in 2005, when a camera-trap campaign designed for ocelots (*Leopardus pardalis*) was conducted between January and March (Ayala et al. 2010). At each site, 21–149 stations were selected to adequately cover study areas ranging from 28–431 km^2 (Table 1), with stations typically active for 30–60 days. Between 2001 and 2009, we mainly employed Camtrakker® (Camtrakker, Watkinsville, Georgia, USA) film camera traps (400 ASA print film), complemented by DeerCam® (DeerCam, Park Falls, Wisconsin, USA), TrailMaster® (TrailMaster, Lenexa, Kansas, USA), and Leaf River® (Leaf River, Taylorsville, Massachusetts, USA) film camera traps. Between 2011 and 2024, we predominantly used Reconyx HC500®, HC550®, and XP2X® digital camera traps, as well as Bushnell® HD 119477 digital camera traps. Between 2001 and 2009, camera-trap stations were not baited, but from 2011 to 2024, they were baited with Chanel No. 5™ or Calvin Klein Obsession™.

We used two camera traps at each station to photograph wildlife from two angles, with cameras positioned opposite each other, approximately 40–50 cm from the ground, and at least 1 m from the area where we expected the jaguar to pass. Film cameras functioned continuously, 24 hours a day, with a 5-min minimum between photographic events, while digital camera traps were programmed to take 10 photographs at each detected event. We visited each station every 5–7 days to change film and batteries. We defined a trap night as a 24-hour monitoring period at a single camera station, with at least one functioning camera. Cameras recorded the day and time for each photograph, with each classified into one of four categories according to the hourly time stamp, as well as sunrise and sunset records for each site (TuTiempo.net): a) **Dawn**, 30 min before daybreak (sunrise); b) **Day**, at sunrise; c) **Dusk**, after sunset but before complete darkness; d) **Night**, 30 min after sunset. For short-eared dogs, we estimated diel activity using kernel density functions, which produce a continuous probability distribution of activity ('Density') rather than raw event counts.

Photographic identifications of *Atelocynus microtis* versus *Cerdocyon thous* were based on clearly distinguishable morphological traits captured by the camera traps. *Atelocynus microtis* has a relatively low body profile, short legs, very small and rounded ears, a large head, and a dense, dark coat ranging from blackish gray to reddish-brown, with a dark dorsal band and a long, very bushy tail that often drags along the ground. In addition, its paws are partially webbed, a trait

Table 2. Details of camera-trapping survey efforts, including year, survey site, survey type, protected area (PN = National Park, TCO = Tierra Comunitaria de Origen or Indigenous Territory, RN = National Reserve, APM = Municipal Protected Area, ANP = National Protected Area, and RB = Biosphere Reserve), range of months, elevation (m a.s.l.), number of trap stations and nights, survey area (km^2), number of short-eared dog (*Atelocynus microtis*) photos, and number of individual events, as well as a summary of short-eared dog relative abundance, including RAI2 (Relative Abundance Index 2), standard deviation (SD), and lower–upper 95% confidence intervals.

Year	Survey site	Survey type	Protected areas	Months	Elevation	# Stations	# Nights	Area	# Photos	# Ind. events	RAI2	SD	CI 95%	
2001	Tuichi	Jaguar	PN Madidi	Aug–Nov	275–341	47	1,513	53	13	7	0.47	0.39	0.01	1.39
2002	Tuichi-Hondo	Jaguar	PN Madidi	Jun–Sep	250–341	66	2,116	213	14	9	0.42	0.20	0.09	0.85
2003	Quendeque	Jaguar	PN Madidi	Aug–Sep	343–380	32	1,108	37	0	0	–	–	–	–
2004	Upper Madidi	Jaguar	PN Madidi	Jun–Aug	249–307	26	1,138	111	9	9	0.80	0.75	0.01	2.37
2005	Heath	Jaguar	PN Madidi, PN Bahuaja Sonene	Jul–Sep	208–198	63	1,813	103	6	6	0.33	0.22	0.01	0.82
2005	Hondo	Ocelot	PN Madidi	Jan–Mar	254–269	36	1,566	28	4	4	0.33	0.15	0.08	0.68
2006	Undumo-Tequeje	Jaguar	TCO Tacana	Aug–Oct	170–183	59	1,640	123	0	0	–	–	–	–
2007	Tambopata	Jaguar	RN Tambopata	Jul–Nov	222–290	138	3,739	247	40	36	0.69	0.26	0.16	1.39
2008	Tuichi-Hondo	Jaguar	PN Madidi	Jun–Sep	250–341	77	2,123	355	21	17	0.81	0.35	0.23	1.61
2008	Quiquibey	Jaguar	RB Pilon Lajas	Sep–Oct	237–259	21	554	57	4	3	0.53	0.29	0.01	1.26
2009	Lower-Mid Madidi	Biodiversity	APM Ixiamas	May–Nov	171–183	44	1,182	162	0	0	–	–	–	–
2011	Upper Madidi	Jaguar	PN Madidi	Jul–Aug	249–307	49	1,909	189	406	43	2.21	0.94	0.76	4.35
2011	Upper Heath	Jaguar	PN Madidi	Oct–Nov	229–258	43	1,470	135	215	24	1.68	0.35	1.02	2.39
2012	Tuichi-Hondo	Jaguar	PN Madidi	Jun–Sep	250–341	89	2,805	376	740	70	2.40	0.87	0.93	4.31
2012	Tuichi Chalalan	Jaguar	PN Madidi	Oct–Nov	308–340	45	1,433	157	315	26	1.79	0.78	0.49	3.49
2014	Tuichi-Hondo	Jaguar	PN Madidi	Ago–Nov	250–341	95	3,634	378	317	35	0.96	0.36	0.33	1.75
2015	Upper Madidi	Jaguar	PN Madidi	Oct–Nov	249–307	57	922	213	218	22	1.34	0.38	0.67	2.08
2015	Pampas Apolo	Biodiversity	PN Madidi	Jun	1,691–2,336	59	482	65	0	0	–	–	–	–
2015	Sipia	Biodiversity	PN Madidi	Jul–Jul	740–786	53	644	34	0	0	–	–	–	–
2016	Mojon-Santiago	Jaguar	APM Pampas del Yacuma	Sep–Nov	265–230	60	1,913	132	0	0	–	–	–	–
2016	Upper Hondo	Biodiversity	PN Madidi	Apr–May	301–419	34	371	15	10	1	0.28	0.18	0.01	1.08
2016	Mamacona	Biodiversity	PN Madidi	Jun–Jul	1,521–2,123	28	312	20	0	0	–	–	–	–
2016	Death Road	Biodiversity	PN Cotapata	Nov–Dec	1,670–3,049	28	515	14	0	0	–	–	–	–
2017	Heath	Jaguar	PN Madidi	Jun–Jul	208–198	69	1,879	208	36	3	0.18	0.13	0.01	0.46
2017	Sarayoj	Biodiversity	PN Madidi	Sep	1,157–1,448	20	136	9	0	0	–	–	–	–
2019	Tuichi-Hondo	Jaguar	PN Madidi	Ago–Nov	250–341	149	6,539	324	978	111	1.39	0.39	0.73	2.25
2019	Quiquibey	Jaguar	RB Pilon Lajas	Jun–Jul	237–259	59	2,533	44	72	7	0.29	0.12	0.08	0.52
2021	Grandes Lagos Tectonicos	Biodiversity	ANP	Ago–Sep	149–157	48	1,106	560	0	0	–	–	–	–
2021	San José Uchupiamonas	Occupancy	PN Madidi	Oct–Dec	405–454	106	4,824	315	222	35	0.74	0.17	0.43	1.11
2022	Upper Madidi	Jaguar	PN Madidi	Ago–Nov	249–307	80	5,296	332	623	66	1.41	0.35	0.78	2.17
2022	Reyes Santa Rosa	Biodiversity	APM Pampas del Yacuma	Jun–Jul	170–179	42	679	776	0	0	–	–	–	–
2023	Tuichi-Hondo	Jaguar	PN Madidi	Jun–Nov	250–341	103	6,538	431	355	44	0.90	0.29	0.41	1.51
2023	Yata, Biata, Benicito	Biodiversity	ANP	Ago–Sep	160–170	32	364	1,323	0	0	–	–	–	–
2024	Isiboro, Pogije, Anteojos	Biodiversity	APM Gran Mojos	Jul–Ago	165–175	43	504	47	0	0	–	–	–	–
Total						**2,000**	**65,300**	**–**	**4,635**	**594**				

unique among Amazonian canids. In contrast, *Cerdocyon thous* displays a compact body with more slender limbs, proportionally larger, rounded ears, a predominantly gray-brown coat with reddish areas on the face and legs, and a black stripe along the dorsal line, as well as dark limbs and a dark tail tip. Although its tail is bushy, it is proportionally shorter relative to body length than that of *A. microtis*, and its overall silhouette is more slender with relatively long legs. These differences in coloration, body proportions, ear shape, dorsal pattern, and tail morphology allowed reliable discrimination between the two species in both nocturnal and diurnal images. Initial camera-trap images from 2001 and 2002 were subsequently confirmed by expert review from Louise Emmons, Renata Leite Pitman, and Damian Rumiz. In any case, we did not detect crab-eating foxes with camera traps in northern La Paz Department; we only detected them in the Beni Department.

Camera-trapping relative abundance was calculated for short-eared dogs following O'Brien et al. (2003), with RAI2 (Relative Abundance Index 2) equal to the number of independent (ind.) photographic events per 100 days. An event was considered independent when a) consecutive photographs from the same camera had clearly distinguishable and different short-eared dog individuals; b) consecutive photographs from the same camera had short-eared dogs separated by at least 30 min; and c) nonconsecutive photographs from the same camera of short-eared dogs.

To better understand population density in the short-eared dog, we also calculated RAI2 for the ocelot (*Leopardus pardalis*), a comparable-sized terrestrial mesocarnivore, which was photographed during these surveys. While ocelots can be slightly larger (5–13 kg) than short-eared dogs (6.5–10 kg) (Noss et al. 2010; Wallace et al. 2010a), both have comparable home ranges (8 km^2 short-eared dog; 1.2–8.1 km^2 ocelot: R. Leite Pitman, pers. comm.; Emmons 1988). However, unlike short-eared dogs, ocelots have distinct rosette patterns that allow individual identification, enabling density estimates using mark-recapture methods (Ayala et al. 2010; WCS, unpublished data).

Biodiversity surveys

We also used camera traps to inform biodiversity surveys at seven sites in the Greater Madidi-Tambopata Landscape and four sites in the Llanos de Moxos Biocultural Landscape (Table 2). For biodiversity surveys, one camera was placed at each station, with 20–59 stations selected opportunistically across the study sites, which ranged from 9 to 1,323 km^2 (Table 2). A single film or digital camera was set and programmed, as described for jaguar surveys above, with 10 of the 11 biodiversity stations baited with perfume.

Occupancy analyses

Firstly, we calculated naïve occupancy, which is simply the proportion of camera traps that detected short-eared dogs in each survey. Then, to analyze detection probability and occupancy for short-eared dogs with camera-trap data from each jaguar survey, we used a single-season, four-occasion occupancy model, which consists of two main processes: a latent (unobservable) ecological process (i.e., true but unknown state of species presence at a site) and an observation process (i.e., observed detection/non-detection data). Multiple occasions (n = 4) are

used to separate the true occupancy state (ψ) from the detection probability (*p*) using a pattern of detection across occasions (detection history). With the latent occupancy, $z_i \sim$ Bernoulli(ψ_i), ψ_i is the probability that site *i* is occupied, which depends on site-specific covariates, and z_i is the true (latent) occupancy state for site *i*, with $z_i = 1$ if the species is present and $z_i = 0$ if it is absent. With the observation or detection history, $y_{ij} \sim$ Bernoulli($z_i \times p_{ij}$); y_{ij} is the observed result (detection/non-detection) at site *i* during occasion *j* ($n = 4$), with $y_{ij} = 1$ if detected and $y_{ij} = 0$ if not detected; p_{ij} is the probability of detecting the species at site *i* during occasion *j*, given the species is truly present; and the product $z_i \times p_{ij}$ is the probability of detection, $p_{ij,}$ if the site is occupied ($z_i = 1$) and 0 if the site is not occupied ($z_i = 0$).

Null model occupancy is the occupancy calculation that does not consider any covariables. Then, considering imperfect detection of short-eared dog presence, we explored the influence of factors that could affect occupancy at the scale of use (1 km^2) with two linear-logit models: logit (p_{ij}) = $x_{ij}\alpha$ (logistic regression used to model the probability of a binary outcome) and logit(ψ) = $x_j\beta$ (logistic regression used to estimate probability of species occupancy (ψ) at a given station). With these formulas, x_{ij} is a vector of variables that vary by site and visit, and α and β are the associated regression coefficients.

We modeled detection probability as a function of five variables related to the detectability of short-eared dogs: 1) number of camera traps deployed at a station (a single or pair); 2) average age of the camera traps deployed at a station, as camera performance may deteriorate over time; 3) average number of days the cameras functioned at each station; 4) whether the camera station was placed in a forest or another habitat type (river, beach, or savanna); and 5) which perfume (Chanel or Calvin Klein) was used as a feature at each station (after 2011).

Initially, we modeled occupancy as a function of 12 covariates related to natural or anthropogenic features that could affect short-eared dog presence: 1) distance to major river (Beni and Madre de Dios); 2) distance to primary river (Hondo, Madidi, Tuichi, Quendeque, Quiquibey, and Tambopata); 3) distance to secondary river; 4) distance to municipal capital; 5) distance to nearest human settlement; 6) distance to nearest tourism lodge; 7) accessibility to site in days; 8) average slope in 1 km^2 cell around the camera-trap station; 9) % forest in 1 km^2 cell around the camera-trap station; 10) % forest in 9 km^2 cell around the camera-trap station (this area corresponds to the estimated home range for the species (Leite Pitman, pers. comm.)); 11) % edge in 1 km^2 cell around the camera-trap station; and 12) % edge in 9 km^2 around the camera-trap station. We calculated these covariates using GIS tools, with all continuous variables standardized to have a mean of 0 and a variance of 1. We selected the best-averaged models of short-eared dog occupancy with ΔAIC < 2 (Arnold 2010). We ranked and rated all variables in the models based on the cumulative QAICw, which was corrected for the *c*-hat (ĉ) test.

We used a two-step approach for model fitting to reduce the number of potential models (Karanth et al. 2011). First, exploratory models incorporated sampling covariates one at a time until all were included and then selected the best occupancy model. Second, we fixed the best detection model, incorporated site covariates one at a time, and selected the best occupancy model. For each step, we used as many factor combinations as possible to evaluate each factor's effect. We performed model fitting in PRESENCE (Hines 2014).

We used bootstrap to assess overall model fit and calculated overdispersion using the ĉ test to adjust for model selection (MacKenzie and Bailey 2004). We used the Akaike Information Criterion (AIC) and the quasi-Akaike Information Criterion (QAIC) for model selection, which is standard practice for dealing with model misfit (Kéry and Royle 2016), and AIC weights for the model average.

Results

Distribution

We gathered 500 short-eared dog records across Bolivia, providing sufficient information to georeference 446 points spanning 1995 to 2024 (Fig. 1). While the initial altitudinal range was 150–1,500 m a.s.l., this expanded to 105–1,945 m a.s.l. after assigning altitudes to locations lacking this information. Most records were from camera traps (*n* = 268; 53.6%), with museum specimens (*n* = 2; 0.4%), direct observations (*n* = 19; 3.8%), and footprints (*n* = 5; 1%) all < 5%. Unfortunately, due to concerns about possible misidentification, with the short-eared dog confused with *Cerdocyon thous* (crab-eating fox), all points derived from questionnaires and local reports were excluded from analyses (*n* = 206; 41.2%).

In total, across all camera-trap surveys, we obtained 4,635 photos that represented 594 independent short-eared dog events during 21 (61.8%) of the 34 camera-trap surveys or 11 (47.8%) of 23 survey sites (Table 2), with photographs in both floodplain and escarpment piedmont forests across an altitudinal range of 166–293 m a.s.l. Short-eared dogs were not recorded with camera traps outside of conservation management units and were also more prevalent in national protected areas that overlap with Indigenous territories (*n* = 339; 57.1%) and national protected areas (*n* = 210; 35.3%), compared to Indigenous territories (*n* = 45; 7.6%) (Fig. 2).

To date, all confirmed short-eared dog records in the Greater Madidi-Tambopata Landscape (*n* = 251) have been in forests < 650 m a.s.l. (Fig. 1), which we consider prime habitat for the short-eared dog. Short-eared dogs were not recorded at the Quendeque, Undumo-Tequeje, Lower-Mid Madidi, Pampas Apolo, Sipia, Mojon-Santiago, Mamacona, Death Road, Sarayoj, Grandes Lagos Tectónicos, Reyes-Santa Rosa, Yata-Biata-Benicito, and Isiboro-Pogije-Anteojos survey sites. For the La Paz Department, there were also 175 records from questionnaires and local reports. In addition, participating researchers observed short-eared dogs on five occasions during camera-trapping campaigns: 1) on a beach of the Tuichi River at approximately 1745 h, 2) along a forest trail in the Tuichi Valley at 1030 h, 3) along a forest trail on the Hondo River at 1130 h, 4) on the road to Upper Madidi at around 1000 h, and 5) on a transect at Upper Heath at 1050 h.

Distribution coverage across the rest of Bolivia was rather sparse (Fig. 1), although short-eared dogs were found across most of the major Amazonian vegetation types < 1,950 m a.s.l. Across the Departments of Beni, Cochabamba, Pando, and Santa Cruz, there were 57 short-eared dog presence records, including local reports (*n* = 31), as well as museum specimens (*n* = 2), camera-trap records (*n* = 18), and direct observations (*n* = 6). Additional insight can be gained by examining each of these four departments individually. First, in the Beni Department, seven camera-trap records occur at < 280 m a.s.l. in pre-Andean Amazonian forest areas (ORE 2022; Fernández et al. 2024), with an

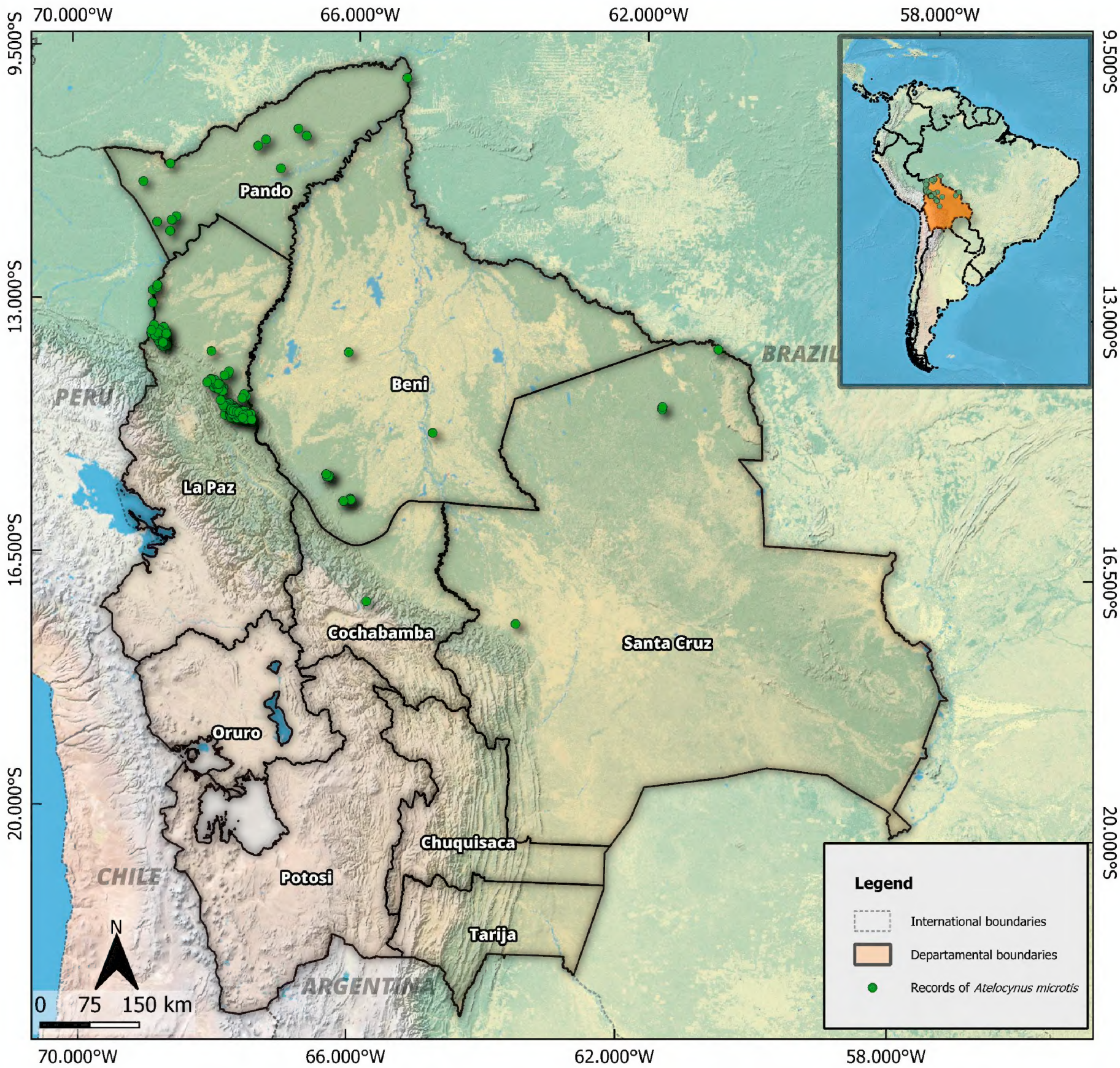

Figure 1. Georeferenced distribution points (*n* = 269), including museum specimens (*n* = 2), direct observations (*n* = 19), and camera-trap photos (*n* = 248), for short-eared dogs (*Atelocynus microtis*) in Bolivia.

additional three camera-trap records between 150 and 280 m a.s.l. in the Llanos de Moxos region across two municipalities: Rurrenabaque, and Santa Ana de Yacuma. In addition, in 2023, there was an unusual sighting and subsequent capture of a juvenile in the city of Trinidad (Erbol 2023). The Beni Department also provided 23 records of short-eared dogs from local reports and questionnaires about five municipalities: Exaltación, Magdalena, Reyes, Rurrenabaque, and San Ramón, at elevations between 134 and 357 m a.s.l.

Second, in the Cochabamba Department, there were only three records, with two local reports from pre-Andean Amazonian forests between 327–475 m a.s.l. in Carrasco National Park and a museum specimen recorded at 1,826 m a.s.l. in the municipality of Villa Tunari.

Third, in the Pando Department, there are three camera-trap records from 102–287 m a.s.l. in pre-Andean Amazonian forests at the Área Modelo de Manejo Integral Santa Rosa del Abuná, a municipal protected area (ACEAA 2022; Guerra Torrez et al. 2023), as well as four camera trap photographs by park rangers

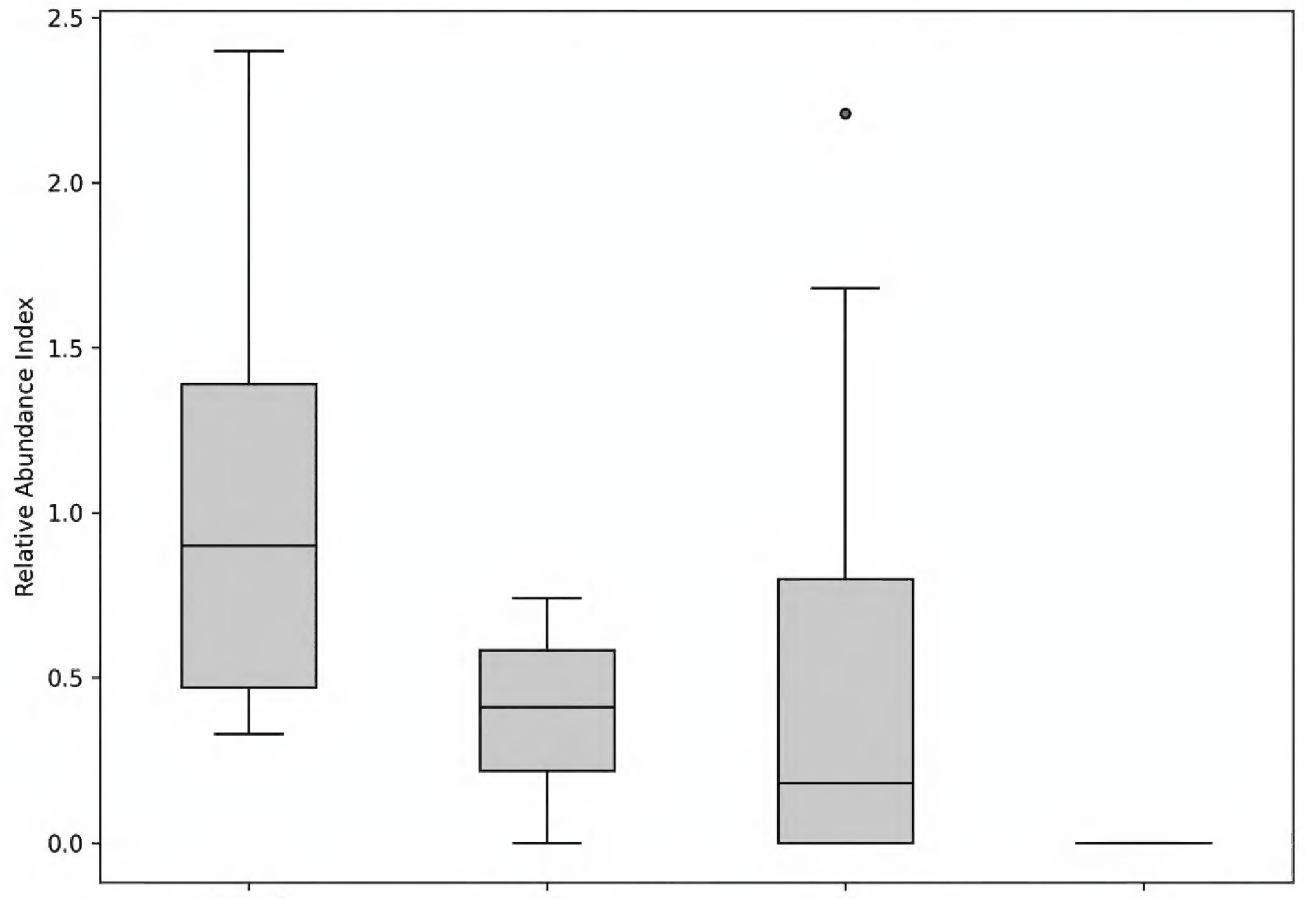

Figure 2. Boxplot of RAI2 (Relative Abundance Index 2) by land management type (protected areas overlapping with Indigenous territories (PA+IT), protected areas (PA), Indigenous territories (IT), and unprotected areas (UA) in Bolivia for the short-eared dog (*Atelocynus microtis*), as derived from independent camera-trap events (*n* = 594).

in Reserva Nacional de Vida Silvestre Amazónica Manuripi, a national protected area, and one local report from the same protected area at 281 m a.s.l.

Finally, in the Santa Cruz Department in eastern Bolivia, there are three records in the pre-Andean Amazon region and the sub-ecoregion of Amazonian forests, including a camera-trap photo from the Bajo Paraguá Municipal Protected Area at 250–260 m a.s.l. (Arispe and Venegas 2015), a direct observation in Noel Kempff Mercado National Park at 182 m a.s.l., and a specimen record from Buena Vista. There are also five local reports in the municipalities of Carmen Rivero Torrez, San Ignacio de Velasco, and San Rafael (142–231 m a.s.l.).

Activity patterns

The 594 independent short-eared dog photographic events demonstrated a predominantly diurnal activity pattern between 0400 and 2000 h (Fig. 3), with 72% classified as diurnal, 2% as dusk, 4% as dawn, and 22% as nocturnal. Short-eared dogs showed activity peaks during the day between 0600 and 1200 h, with fluctuating but slightly lower levels of activity thereafter until 2000 h. Activity levels were very low between 2000 and 0400 h, then increased slightly between 0400 and 0600 h.

Relative abundance

Camera-trapping capture rates (RAI2: Table 2) revealed that short-eared dog relative abundance across surveys was approaching significance ($H = 17.02$, $gl = 10$, $p = 0.07$). Short-eared dog relative abundance was highest in the Tuichi-Hondo valleys in 2012 (2.40 ind. events per 100 trap nights), at the Upper Madidi River in 2011 (2.21 ind. events/100 trap nights), at Tuichi Chalalan in 2012 (1.79 ind. events/100 trap nights), and at Upper Heath River in 2011 (1.68 ind. events/100

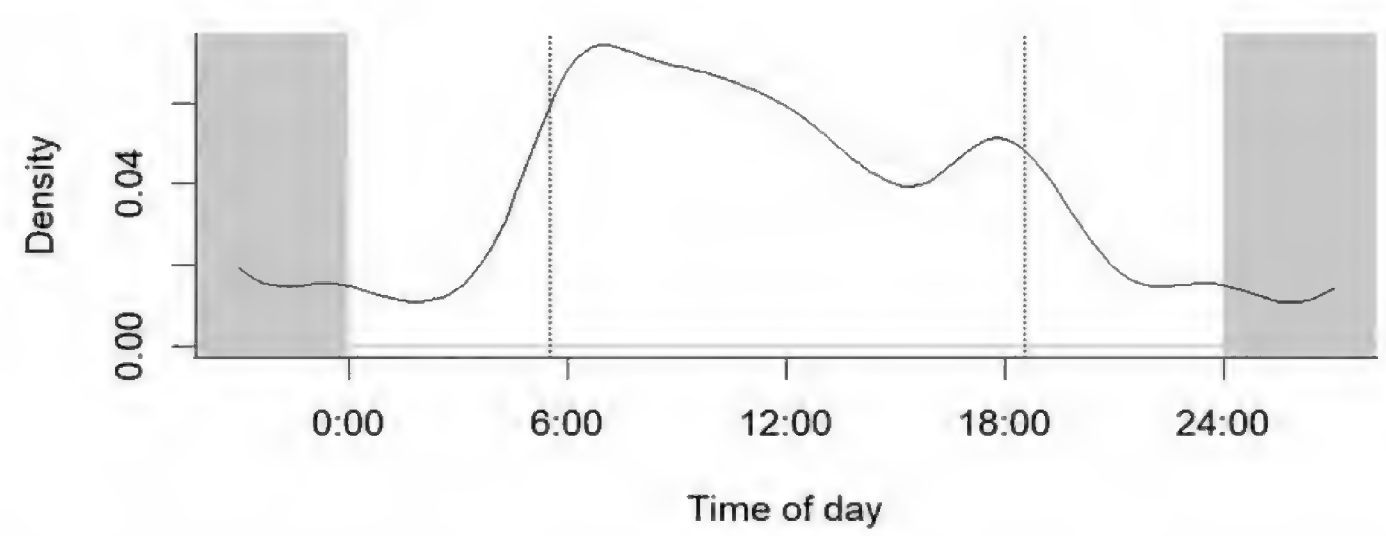

Figure 3. Short-eared dog (*Atelocynus microtis*) activity pattern in Bolivia derived from independent camera-trap events (n = 594). Density (y-axis) corresponds to the kernel density estimation of activity, where values indicate the relative probability of activity across the 24 h cycle (x-axis). This representation is normalized (area = 1) and does not reflect raw counts, but rather the concentration of activity at specific times.

trap nights). Three sites where presence was confirmed (Quiquibey, San José de Uchupiamonas, and Tambopata) had intermediate relative abundances between 0.5 and 1 ind. events per 100 trap nights, and two sites had lower relative abundances (Heath and Upper Hondo) of < 0.5 ind. events per 100 trap nights.

We were able to gather longitudinal data on short-eared dog relative abundance at four sites (Table 2). First, in the Tuichi-Hondo valleys, relative abundance remained stable for the first decade (2001: 0.46 ind. events/100 trap nights; 2002: 0.4 ind. events/100 trap nights; 2008: 0.81 ind. events/100 trap nights), before increasing significantly in 2012 (2.4 ind. events/100 trap nights), and then dropping to a stable intermediate level in 2014, 2019, and 2023 (0.96, 1.39, and 0.9 ind. events/100 trap nights). Second, at the Upper Madidi site, the relative abundance of short-eared dogs was 0.8 ind. events per 100 trap nights in 2004, then markedly higher in 2011 (2.21 ind. events/100 trap nights), and then dropping to a stable intermediate level in 2015 and 2022 (1.34 and 1.41 ind. events/100 trap nights). Third, for the Quiquibey River, capture rates were relatively low in 2008 and 2019 (0.53 and 0.29 ind. events/100 trap nights, respectively). Finally, for the Heath River, capture rates were notably lower in 2005 and 2017 (0.33 and 0.18 ind. events/100 trap nights). Across these four sites, with all data combined, short-eared dog relative abundance varied between 0.33–0.81 ind. events/100 trap nights between 2001 and 2008 (mean = 0.55), between 1.68–2.4 ind. events/100 trap nights between 2011 and 2012 (mean = 2.02), and between 0.18–1.41 ind. events/100 trap nights (mean = 0.83) from 2014 onward (Table 2).

At sites where both ocelots and short-eared dogs were present, ocelot camera-trap capture rates varied between 0.87 and 6.91 ind. events/100 trap nights (Table 3). On average, camera-trap capture rates for short-eared dogs were only a quarter (25.9%) of those for the more common ocelot, although this ranged between 5–58.7% (Table 3).

Occupancy

Occupancy analyses revealed that short-eared dog detection probability ranged from 0.01 to 0.75, with typical values between 0.1 and 0.41 (Table 4). While these probabilities were positively influenced a single time in 2012 by the mean

number of days camera traps were active at a station and a single time in 2022 by whether the camera-trap station was placed in a forest, no other detection covariates were considered relevant across 18 camera-trap surveys where short-eared dogs were detected (Table 4). In contrast, short-eared dog occupancy was positively influenced by five different covariates across the camera-trap surveys (Table 4): 1) distance to the primary river (i.e., larger occupancy values as distance to the river increased) (two surveys); 2) distance to the nearest human settlement; 3) distance to the nearest tourism lodge; 4) % forest in the 1 km^2 cell around the camera-trap station (four surveys); and 5) % forest in the 9 km^2 cell around the camera-trap station. In addition, short-eared dog occupancy was negatively influenced by one covariate: % edge within a 9 km^2 area around the camera-trap station (two surveys). Occupancy values ranged from 0.03 to 0.43 across the camera-trap surveys but were typically 0.18–0.4 (Table 4).

By combining data from different sites across relatively short time frames (Table 5), we were able to build more robust occupancy models with multiple covariables. These models were relatively consistent over time, with short-eared dog detection probability varying between 0.1 and 0.32 and positively influenced by whether the camera trap was placed in a forest (two of six combined analyses). Three different covariates positively influenced short-eared dog occupancy: 1) distance to the primary river (two combined analyses), 2) % forest in the 1 km^2 cell around the camera-trap station (two combined analyses), and 3) % forest in the 9 km^2 cell around the camera-trap station (two combined analyses). In addition, in one combined analysis, short-eared dog occupancy was negatively influenced by one covariate, % edge in the 1 km^2 cell around the camera-trap station. Occupancy values varied between 0.24 and 0.46 (Table 5).

Table 3. Camera-trapping relative abundance indices (RAI2) for short-eared dogs (*Atelocynus microtis*) compared with ocelots (*Leopardus pardalis*) across 21 camera-trapping surveys where both species were recorded in Bolivia.

Year	Survey site	RAI2 Short-eared dog	RAI2 Ocelot	Proportion RAI2 Short-eared dog/Ocelot
2001	Tuichi	0.47	2.88	0.16
2002	Tuichi-Hondo	0.42	3.59	0.12
2004	Upper Madidi	0.80	1.73	0.46
2005	Heath	0.33	2.40	0.14
2005	Hondo	0.33	2.20	0.15
2007	Tambopata	0.69	1.94	0.36
2008	Quiquibey	0.53	3.40	0.16
2008	Tuichi-Hondo	0.81	4.03	0.2
2011	Upper Heath	1.68	4.93	0.34
2011	Upper Madidi	2.21	5.01	0.44
2012	Tuichi Chalalan	1.79	3.36	0.53
2012	Tuichi-Hondo	2.40	4.70	0.51
2014	Tuichi-Hondo	0.96	3.24	0.3
2015	Upper Madidi	1.34	4.37	0.31
2016	Upper Hondo	0.28	0.87	0.32
2017	Heath	0.18	3.28	0.5
2019	Quiquibey	0.29	5.76	0.5
2019	Tuichi-Hondo	1.39	4.49	0.31
2021	San José Uchupiamonas	0.74	1.26	0.59
2022	Upper Madidi	1.41	6.70	0.21
2023	Tuichi-Hondo	0.90	6.91	0.13
Mean		**0.95**	**3.67**	**0.26**

Table 4. Short-eared dog (*Atelocynus microtis*) detection probability, naïve and null occupancy, and averaged best occupancy model, with influencing variables (positive or negative), for 18 camera-trap surveys in northwestern Bolivia and southeastern Peru.

Year	Survey site	ψ Naive	p Null	ψ Null	Averaged best model plus influencing covariates	p	SD	ψ	SD	LCL	UCL	c/hat
2001	Tuichi	0.09	0.15	0.18	Null	0.15	0.13	0.18	0.15	0.03	0.61	–
2002	Tuichi-Hondo	0.12	0.03	–	Null	0.03	0.01	–	–	–	–	–
2004	Upper Madidi	0.04	0.75	0.04	Null	0.75	0.22	0.04	0.04	0.01	0.23	–
2005	Heath	0.06	0.02	–	Null	0.02	0.01	–	–	–	–	–
2007	Tambopata	0.14	0.17	0.27	ψ: distance human settlement & distance nearest tourism lodge (both positive) ψ: % edge 9 km² (negative)	0.17	0.07	0.28	0.16	–	–	0.83
2008	Tuichi-Hondo	0.17	0.05	–	Null	0.17	0.05	–	–	–	–	–
2008	Quiquibey	0.14	0.04	–	Null	0.14	0.04	–	–	–	–	–
2011	Upper Madidi	0.27	0.4	0.3	ψ positive: % forest 9 km²	0.4	0.08	0.31	0.09	0.16	0.54	1.12
2011	Upper Heath	0.42	0.11	–	Null	0.11	0.02	–	–	–	–	–
2012	Tuichi-Hondo	0.24	0.42	0.27	3 model average (ψ: distance primary river (positive); p: mean # days camera active (positive); ψ: % forest 1 km² (positive))	0.39	0.06	0.28	0.19	–	–	0.61
2012	Tuichi Chalalan	0.22	0.27	0.31	Null	0.27	0.09	0.31	0.11	–	–	–
2014	Tuichi-Hondo	0.16	0.41	0.18	ψ: distance primary river (positive)	0.41	0.08	0.18	0.06	0.09	0.31	0.63
2015	Upper Madidi	0.25	0.2	0.41	ψ: % edge 9 km² (negative)	0.21	0.07	0.4	0.14	0.12	0.65	1.11
2017	Heath	0.03	0.01	–	Null	0.01	0.01	–	–	–	–	–
2019	Tuichi-Hondo	0.31	0.33	0.39	ψ: % forest 1 km² (positive)	0.33	0.06	0.39	0.08	0.25	0.59	1.63
2019	Quiquibey	0.1	0.1	0.29	Null	0.1	0.09	0.29	0.25	0.04	0.82	–
2022	Upper Madidi	0.3	0.28	0.41	ψ: % forest 1 km² (positive), p: forest placement (positive)	0.27	0.04	0.43	0.12	–	–	1.17
2023	Tuichi-Hondo	0.22	0.17	0.43	ψ: % forest 1 km² (positive)	0.18	0.05	0.41	0.12	0.2	0.68	0.78

Table 5. Short-eared dog (*Atelocynus microtis*) detection probability, naïve and null occupancy, and averaged best occupancy model, with influencing variables (positive or negative), for six combined camera-trap analyses in northwestern Bolivia and southeastern Peru.

Years	Survey sites	ψ Naive	p Null	ψ Null	Winning model	p	SD	ψ	SD	LCL	UCL	c/hat
2002–2005	Tuichi-Hondo, Upper Madidi, Heath	0.08	0.09	0.26	ψ: % forest 1 km² (positive), p: two cameras (positive)	0.11	0.04	0.24	0.09	0.09	0.46	1.13
2007–2008	Tambopata, Tuichi-Hondo, Quiquibey	0.15	0.11	0.41	ψ: % forest 9 km² (positive)	0.1	0.04	0.44	0.16	0.14	0.7	0.54
2011–2012	Upper Madidi, Upper Heath, Tuichi-Hondo, Tuichi TCO	0.27	0.3	0.36	ψ: % forest 9 km² (positive)	0.23	0.04	0.44	0.07	0.32	0.59	1.47
2014–2015	Tuichi-Hondo, Upper Madidi	0.19	0.32	0.25	ψ: edge 1 km² (negative), distance primary river (positive)	0.32	0.05	0.24	0.06	0.14	0.39	0.83
2017–2019	Heath, Tuichi-Hondo, Quiquibey	0.17	0.28	0.23	2 model average (p: forest placement (positive), ψ: distance primary river (positive); p: forest (positive))	0.21	0.12	0.31	0.07		–	1.64
2022–2023	Upper Madidi, Tuichi-Hondo	0.26	0.23	0.4	2 model average (p: forest placement (positive); ψ: forest 1 km² (positive))	0.2	0.06	0.46	0.08	–	–	1.05

Discussion

This study was built on initial distribution maps for the short-eared dog in Bolivia (Wallace et al. 2010a, 2013a, 2013b), with this species apparently absent from the drier tropical forests of southern lowland Bolivia but present in humid Amazonian forests < 2,000 m a.s.l. across central and northern lowland Bolivia. When we excluded local reports and interview data from the distribution data due to potential misidentification, the resulting distribution was sparse across the lowlands, with concentrations at sites in northern La Paz Department, where camera-trap efforts have been intensive. Because camera-trapping

efforts have been extremely limited in the Andean foothill and montane forests of the landscape between 650 and 1,950 m a.s.l., photographic confirmation of short-eared dog presence is not yet available in those forests.

The short-eared dog was confirmed to be primarily diurnal and crepuscular, with some nocturnal activity in the early evening and before dawn, which aligns with previous studies (Gómez et al. 2005; Leite Pitman et al. 2026). Our occupancy analyses underline the preference of short-eared dogs for intact forest (Rocha et al. 2020; Leite Pitman et al. 2026), a preference further emphasized by the fact that many individual and collective analyses include forest cover or edge density around the camera-trap station as significant covariates. Our occupancy analyses also suggest that short-eared dogs prefer *terra firme* forests over riverine forests, as occupancy increased with distance from the river in two individual surveys and two combined analyses. This provides further support for preliminary results from southern Peru (Leite Pitman et al. 2026; Zwicker, unpublished data).

This study represents the largest collection of confirmed short-eared dog records anywhere within the species' distribution (Leite Pitman and Williams 2011; Leite Pitman et al. 2026). Camera-trap stations were purposely placed along river beaches (22% of locations) to increase jaguar detectability. In fact, the short-eared dog showed the inverse pattern to jaguars, with almost all (98.3%) independent events at camera-trap stations placed in the forest and the remainder along streams and rivers in the forest. Even though intensive camera-trap surveys, with higher numbers of trap stations and capture nights sampled, will logically increase the probability of registering rarer terrestrial species, our camera-trap capture rates suggest that, at least in some areas, short-eared dogs are not as scarce as previously thought (Ginsberg and Macdonald 1990; Leite Pitman et al. 2026). Our results also imply that short-eared dog relative abundance may vary over time. Although we have no evidence to explain what drives these temporal variations, it is important to highlight that previous publications have suggested that domestic dog diseases may have negatively affected short-eared dog populations (Leite Pitman et al. 2003, 2026).

Based on average RAI2 values, short-eared dog relative abundance was about a quarter that of ocelots. Population density estimates for ocelots were 66 individuals/100 km^2 at Hondo (2005; Ayala et al. 2010) and 55 individuals/100 km^2 in the Tuichi (2023; WCS, unpublished data); thus, short-eared dogs were extrapolated to have an average density of approximately 15 individuals/100 km^2. This density estimate was much lower than the 0.5 individuals/km^2 estimated through telemetry efforts on five animals in southern Peru (Leite Pitman and Williams 2011). Our study strongly suggests that short-eared dogs are typically less abundant than ocelots but more abundant than larger, more visible, and detectable carnivores, such as the jaguar (Wallace et al. 2003; Ayala et al. 2022).

In conclusion, camera-trap surveys provided significant information on the behavior and relative abundance of the short-eared dog, suggesting it is more abundant than previously thought, although it remains a relatively rare medium-sized carnivore. Encouragingly, short-eared dog relative abundance was higher in protected areas and Indigenous territories that overlap with protected areas, reinforcing the importance of these management units for biodiversity conservation. These results have significant conservation implications, suggesting that large areas of continuous forest, comparable in size to larger protected areas, will be required to maintain long-term, viable populations of short-eared dogs.

Acknowledgements

We thank the Gordon and Betty Moore Foundation (GBMF), MacArthur Foundation, Blue Moon Fund, Beneficia Foundation, Disney Wildlife Conservation Fund, Woodland Park Zoological Society, Liz Claibourne & Art Ortenberg Foundation, and Wildlife Conservation Society (WCS) for support for camera-trapping monitoring efforts in the Greater Madidi-Tambopata Landscape and Llanos de Moxos Biocultural Landscape Conservation Programs. We are especially grateful to the Bolivian Protected Area Service (SERNAP), the Bolivian Biodiversity and Protected Area Directorate (DGBAP), the Peruvian Institute for Natural Resources (INRENA), the Madidi, Pilon Lajas, Cotapata, and Tambopata protected area administrations, the Cayetano Heredia University, and the Tacana Indigenous Council (CIPTA), the Lecos de Apolo Indigenous Council (CIPLA), the San Jose de Uchupiamonas Indigenous community, and the Reyes, Santa Rosa, Exaltacion, and Loreto municipalities for research permits and logistical support. We thank the Takana people of northern La Paz Department in Bolivia and the park guards of ANMIN Apolobamba, PN Bahuaja Sonene, PNANMI Madidi, RBTCO Pilon Lajas, and RN Tambopata for kindly providing interview data on short-eared dog sightings. We thank Mauricio Herrera, SERNAP, and the park guards of the Manuripi National Wildlife Reserve for sharing unpublished canid observations. We also thank Heidy Lopez-Strauss, Nohelia Mercado, and Ariel Reinaga for distribution systematization, as well as GIS and map assistance. Finally, we thank Karen DeMatteo and Renata Leite Pitman for their comments, edits, and suggestions for improving the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

Funding

No funding was reported.

Author contributions

Conceptualization: RBW. Data curation: GA, RBW, MV, ZP. Formal analysis: GA, RBW, MV. Funding acquisition: RBW. Investigation: RBW, MV, ZP, GA. Methodology: GA, RBW, MV. Project administration: GA, RBW. Supervision: RBW. Writing – original draft: RBW. Writing – review and editing: MV, GA, RBW, ZP.

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Data availability

All of the data that support the findings of this study are available in the main text.

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